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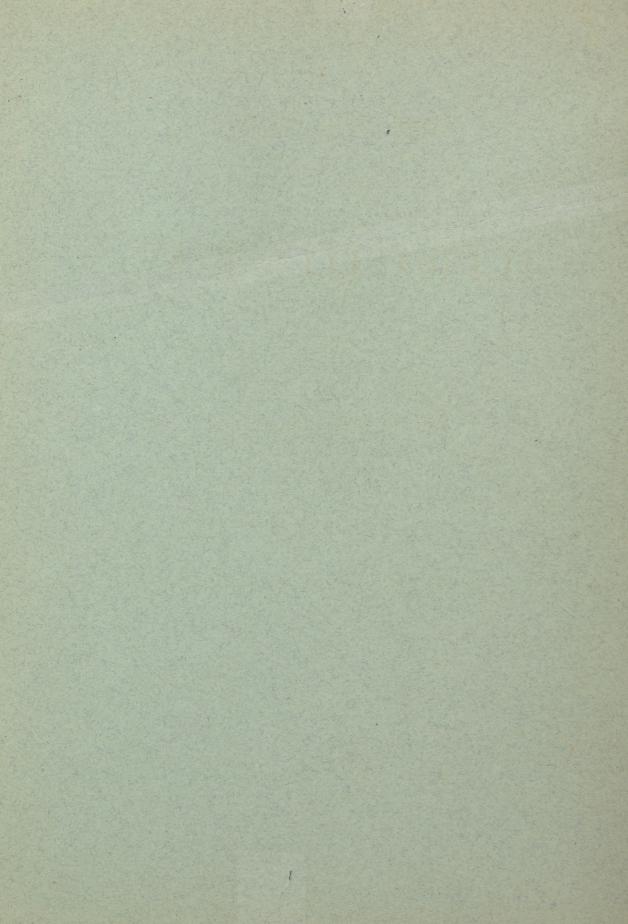
BY

C. O. WHITMAN.

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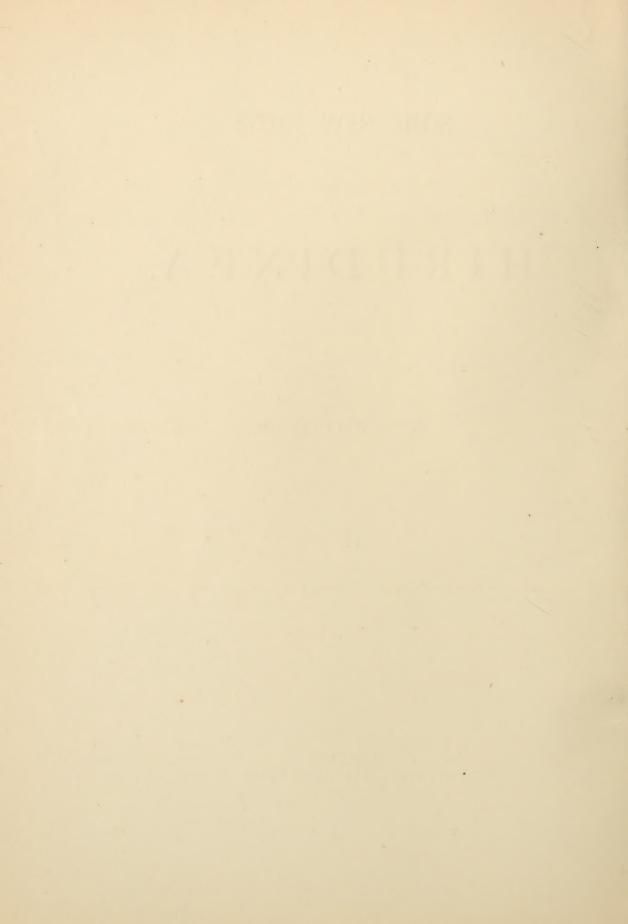
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SOME NEW FACTS ABOUT THE HIRUDINEA.

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A FEW facts and conclusions are here briefly stated in advance of several papers on the *Hirudinea*, which are now nearly completed, and which I hope to see published in the third volume of this JOURNAL.

- I. The *Hirudinea*, as a group, are characterized by the possession of segmental sense-organs on the first ring of every somite. The plan of arrangement is everywhere essentially the same as I have already described in detail for the ten-eyed leeches. The statement by Mr. Apàthy that such organs do not mark the somites in Aulastoma is incorrect; and inexcusably so, as their topography has already been made known. I do not deny that some forms are found, like Nephelis, Clepsine bioculata, and Pontobdella, in which the segmental arrangement has been much obscured, or perhaps entirely obliterated. It is plain that such conditions might be reached in two ways: either by the loss or the multiplication of organs.
- 2. As the metameric arrangement of these sense-organs characterizes marine as well as fresh-water and land leeches, and as they everywhere agree in certain remarkable details of number, topography, and structure, I am led to believe that the diffuse, or non-metameric arrangement, exemplified in *Nephelis* and some other forms, has been secondarily acquired. *Nephelis* is an instructive example, for it shows an analogous departure from the typical arrangement in the multiplication of its testicular organs. The lateral-line organs of some fishes and amphibia illustrate the same point. Obscuration of the metamerism of organs through multiplication is too well known to require further illustration here. The presence of well-developed eyes in *Nephelis*, *segmentally* disposed, points unmistakably to the former possession of the ordinary segmental sense-organs.
- 3. I have brought together a large amount of evidence to prove that in all ten-eyed leeches, including many widely scat-

tered species of both land and fresh-water forms, the eyes represent enlarged and more or less modified segmental sense-organs. The question remains to be answered, whether the same holds true of other leeches. If this be conceded, then I see no easy escape from the conclusion that the metameric sense-organs are earlier in origin than the non-metameric ones. If the scattered organs were first in order of development, we ought at least to find some cases in which the eyes are not segmentally arranged. There are some cases in which the serial homology of the eyes with the segmental sense-organs is not at first sight apparent. This is true of some species of *Clepsine*. The development of the eyes in these cases, as will be shown in one of my papers, settles, *beyond dispute*, the fact that the eyes are segmental in origin, and strictly homologous with the segmental sense-organs.

- 4. In the case of *Clepsine parasitica* and *C. chelydræ* (n.sp.), I have satisfied myself that the segmental sense-organs appear very early in the embryo, before the time of hatching, while the scattered organs arise later. Another evidence in support of the above-stated conclusion.
- 5. In Hæmenteria (commonly, but incorrectly, Hæmentaria), and in several species of Clepsine from Japan and America, there is one somite clearly marked by segmental sense-organs in front of the eyes. This makes twenty-six somites in front of the acetabulum, not counting the narrow tip of the cephalic lobe. Mr. Apathy insists on counting this tip as the first somite, but he has not yet produced any satisfactory grounds for so doing. The difference between us is, not that I deny the possibility of finding one, or even more than one somite in the "prostomial," but that I question the propriety of calling it one, while it still remains undetermined whether it represents one, two, three, or none at all. The argument from the number of segments in the brain will be worth considering when we know precisely how many somites are there represented. The question is beset with some difficulties, which are not likely to be removed by anything less than thorough embryological research. The argument from the labial sense-organs, as will be seen in the next paragraph, is likewise premature.
- 6. The labial sense-organs prostomial sense-organs of Apathy are serially homologous with *ventral* segmental sense-

organs, as I shall be able to show very clearly in *C. chelydra* and in a Japanese species. They do not therefore represent one somite, as supposed by Mr. Apàthy, but merely the ventral organs of as many somites as belong to the cephalic lobe. Their dorsal counterparts have preserved their segmental arrangement. If any dorsal organs are represented in these labial organs, the development ought to show it. I once thought I had found some evidence of this nature, but I have since followed the history of these organs farther, and find reason to modify my view.

7. Systematists have usually concluded that where no eyes could be recognized by surface examination, none were present. My experience leads me to suspect that most of our reputed blind leeches will yet be made to bear testimony to the blindness of their observers. To all outward appearance, Branchelliopsis (gen. nov.), a Japanese marine leech, has no eyes. I made a careful examination of the head, first in a fresh and then in a hardened state, and finally by sections, but found no eyes. Returning to the study of this leech recently, after having learned in what the eye of a leech consists, I succeeded in finding at least two pairs of eyes. These eyes have so little pigment that they cannot be seen from the surface; and any one in search of pigment-spots would find little in sections to arrest the eye. The visual cells, however, are there; and their form and relation to a thin, open background of pigment would, on close examination, entitle them to rank as eyes in the ordinary acceptation of that term as applied to leeches. In form they remind one of the eyes of Piscicola; in structure, the eyes of Clepsine; and in position, the eyes of Nephelis. They are in fact so little removed in general make-up and appearance from the ordinary segmental sense-organ, that I had to examine sections made in the three principal planes before fully satisfying myself that they would pass as veritable leech eyes.

8. Piscicolaria (gen. nov.), a parasite of fishes in the smaller lakes of Wisconsin, about the size of Piscicola, and intermediate in form and structure between Piscicola and Branchelliopsis, comes nearer to being blind than any other leech I have yet examined. The only evidence of an eye is a single large visual cell, on either side of the head, without a trace of a pig-

ment investment. In view of these facts, and others yet to be noticed, we can no longer regard pigment as an essential element of the leech eye. It will not do to fall back on the hypothesis of degeneration, and assume that these eyes supplied with little or no pigment are functionless rudiments. The visual cells are here as perfectly developed as in the pigmented eyes, and the same is true of the optic nerves.

9. The test of a leech eye, then, is the presence of visual cells. Now what are the visual cells, and how are they to be recognized? After spending a good deal of time in the study of the structure and development of the sense-organs of the leech, I feel quite confident of having reached a point in the investigation where I can safely answer these questions. The visual cells are the "large clear cells" of Leydig, the so-called "Glaskörper." The proof of this lies in a variety of facts, only a few of which can here be presented in a summary way. The leading points are as follows: I. These cells always make up the bulk of the eye, and in the Hirudo pattern they are the only cells supplied by the optic nerve. 2. The main axis of these cells that passing through the centre of the cell and the eccentric nucleus — is generally, though not invariably, parallel with the axis of the eye. This is most clearly seen in some species of Clepsine, and is very evident in Branchelliopsis. 3. In these genera, the nucleus lies on the side exposed to the light, the clear rod-like part of the cell being directed towards the pigment. The cells are practically inverted, the nerve-fibres entering at the nucleated pole. 4. A comparison of the different patterns of eye represented in Hirudo, Nephelis, Clepsine, and Branchelliopsis, with the typical segmental sense-organ, shows that the chief distinction between the two classes of organs lies in the relative abundance of the clear cells.

structure and in function. There is an axial cluster of elongated cells, terminating at the surface in minute hairs, and representing most likely a tactile organ. Around and beneath the tactile cells, are the large, clear visual cells, so characteristic of the eye. Thus we have a visual and a tactile organ combined, both derived from a common mass of indifferent epidermal cells, and both supplied by fibres from a common nerve branch.

II. Incredible as the double nature of these organs may at

first appear, there is no escape from the fact, when we once understand the structure of the eye in Clepsine. A vertical section in the plane of the optical axis reveals the compound nature of the eye, and the identity of its structure with that of the segmental sense-organs. Here stands the tactile part of the organ, an exact copy of every feature seen in the corresponding part of a segmental sense-organ; and below and behind, but in continuity with the tactile portion, lies the mass of visual cells. The common nerve runs up in front of the visual cells, dwindling gradually in size as its fibres pass to the cells, and at length it is lost in the tactile cells. The main features of this eye have been known to me for about two years, but it did not seem best to hasten the communication of the facts before giving the whole subject careful study. The sensehairs were first clearly demonstrated in Nephelis, and next in both the young and adult of Clepsine. The nerves supplying the eyes and sense-organs of the head arise in Branchelliopsis and Clepsine from the five sub-œsophageal ganglia.

12. In *Hirudo*, the visual cells are symmetrically placed around the *axial* nerve fibres, and no tactile cells are developed; in *Clepsine* and *Hæmenteria*, the visual cells are developed only on the posterior side of the nerve, while the tactile cells are grouped above and in front. In *Nephelis* the nerve is again axial; in *Branchelliopsis* it is eccentric, as in *Clepsine*, and there are comparatively few visual cells.

13. Both the eyes and the segmental sense-organs develop as local thickenings of the epidermis. At first the cells are alike in form, size, and structure. About the time the pigment begins to appear, the two sorts of sense-cells begin to show a difference in size, and an indistinct boundary line appears between them.

14. The *metameric* arrangement of the sense-organs of the *Hirudinea* is a matter of more importance than the latest writer on the subject, Mr. Apàthy, appears to realize. The limits of this paper do not permit me to review the arguments which this young naturalist has entombed in a *preliminary* report of about eighty pages (portentous dimensions!). I am compelled to remark, however, that this author has not been sufficiently careful in presenting the views of others. As one out of many instances that might be cited, the following is characteristic. I am rep-

resented as having made the supremely ridiculous mistake of taking the wart-like protuberances found on many species of Clepsine for sense-organs. In C. marginata—to cite one more case—I reported four anal ganglia. My statement was made with reference to a single species, and is perfectly accurate; but Mr. A. charges me with an error, because, forsooth, my statement is not true for all leaches. This is the style of criticism indulged in throughout this preliminary monograph. What I have called visual cells are put down, ex cathedra, for "fatcells," "gland-cells," etc. Charity and necessity alike commend us in taking immediate leave of such oracular wisdom. It is to be hoped that before that impending final monograph is launched, our author will have discovered the unregenerate source of his present afflatus.

15. The key to the analytical study of the external form is to be found in the metameric disposition of the sense-organs. Of course internal structure is to be taken into account, and a fair critic would hardly have fallen into the mistake of supposing that I had neglected this side of the subject. I have had considerable opportunity to learn the practical value of this key for systematic purposes, and the longer I use it the more indispensable it proves. The terminal somites are of the highest importance for specific diagnosis, and their annular composition, which offers so much of theoretical interest, cannot be deciphered without the aid of the segmental sense-organs. What clearer demonstration of all this could be desired than has already been furnished in the case of the ten-eyed Hirudinea? I am now prepared to show that the same holds true of both fresh-water and marine Rhyncobdellidæ, although the application of the method is, as a rule, more difficult here than in the Gnathobdellidæ. The number of ventral ganglia is generally supposed to be the same for all the different species, genera, families, and so on for the entire class. While we may be sure that the number of somites represented in the rings does not exceed the number of ganglia, is it not perfectly clear that the latter cannot serve as a guide in determining the annular limits of somites, particularly at the ends of the body? Then it must be remembered that the number of ganglia in the cephalic group has never been satisfactorily determined, and even the number in the caudal group has been variously estimated at six, seven, and eight.

- 16. The importance of the segmental character of the senseorgans is not to be measured by its usefulness in systematic determinations. Levdig showed long ago, in Hirudo, how the same nerve supplies successive sets of eyes. How, then, could the ganglia or nerves of the so-called brain be made to reveal the metameric character of the eyes? And how could the important serial homology of the eyes ever have been determined except through the discovery of their relations to sense-organs known to have a metameric arrangement? It is by virtue of this arrangement that I have succeeded in getting such a complete and convincing picture of the origin and history of the leech eye. Segmental sense-organs are found in other annelids and in vertebrates, but nowhere is the transition from lower to higher sense-organs so perfectly illustrated as in the leech. Branchelliopsis, Clepsine and Hirudo reveal all the intermediate steps, beginning with the purely tactile organ; then advancing to the compound organ, in which a few of the cells have been modified to serve the purpose of vision, while the rest have retained their primitive character; and finally, culminating after a long series of progressive encroachments, — the visual elements increasing gradually at the expense of the tactile, — in an organ in which the original function has been entirely suppressed and a new one substituted for it. Here is a chapter in the evolution of sense-organs so perfectly preserved in all its details as to leave no room for scepticism.
- 17. Without entering into the discussion of the point, I desire to repeat here the suggestion made on another occasion, that the segmental sense-organs of the leech are identical with the lateral-line organs of vertebrates. I do not venture to express such an opinion without having duly reflected on the objections that might be raised. Having spent considerable time in the study of the lateral-line organs in the larval stages of amphibia and marine fishes, and having followed closely the work of my colleague on Amia, Lepidosteus, and various teleostei, I know, at first hand, where the difficulties lie, and I do not think I underestimate their importance.
- 18. Perhaps it will not be venturing too far on speculative ground if, in this connection, another suggestion be offered;

namely, that the segmental sense-organs of annelids have formed the starting-point for the development of the organs of special sense in the higher animals, not excepting even the eyes of ver-The evidence is rapidly growing stronger in favor of the origin of the olfactory and auditory organs from lateralline organs; and the gustatory organs are certainly destined to fall into the same line. Mr. Allis' observations show how lateral-line organs may travel through gill-slits, and the mode of growth of the surface bulbs shows how they may spread to new areas. In regard to the vertebrate eye, we can never expect, of course, to determine its identity with lateralline organs by such direct evidence as is available in tracing the origin of the leech eye. Assuming that vertebrates and annelids have had common ancestors with segmental sense-organs, the fact that such organs have been converted into eyes in at least one large group of annelids, raises the suspicion that nature may have practised the same economy in all branches from the common stock. And when we find strong grounds for thinking that the lateral-line organs have served as the point of departure for the formation of gustatory, olfactory, and auditory organs, our suspicion in regard to the eyes no longer appears incredible. I am not at all unmindful of what might now appear to be an almost insurmountable objection to regarding the vertebrate eye as a segmental organ. As one of my laboratory colleagues is soon to bring some new facts to bear on this subject, and as further discussion might lead to the expression of views that have certainly been corroborated by his observations, I drop the question for the present. I would, however, mention one observation of mine with reference to the eye of Necturus. The basis for the eye is already discernible as a circular area — after treatment with osmic acid followed by Merkel's fluid - long before the closure of the medullary folds of the brain, at a stage corresponding closely with Goette's Fig. 12, Pl. III., of Bombinator igneus.

But we have an *unpaired* vertebrate eye, of recent discovery, but possibly of very ancient origin. How is it possible to apply the hypothesis of segmental derivation here? As segmental sense-organs are always *paired*, it is not easy to account for the origin of an azygous organ from them except through the fusion of at least one pair. We are not able to point to

many indications of a double origin, but the two vesicles in Petromyzon (Ahlborn, Beard), and the double pineal stalk of Varanus giganteus (Spencer), are facts that certainly favor such a view. Moreover, the position of the organ is such that we must suppose it to be derived from two sources, namely, the lateral (sutural) edges of the medullary plate. The fusion of segmental sense-organs has nothing improbable in it, as can be shown by more than one example from the Hirudinea. On the other hand, the origin of organs by division, although claimed by a number of authors of high repute, has not a single verified fact in its favor. I am quite confident that such a process does not underlie the multiplication of lateral-line organs, and I have found nothing of the kind in the development of the segmental sense-organs of the Hirudinea.

The origin of the pineal eye from the lateral eyes, as held by Beard, is open to more serious objections. In the first place, it is difficult to believe that this organ is of later origin than the lateral eyes; and in the second place, the idea that the entire optic vesicles (before and during the closure of the neural plate) represented retinal epithelium does not appear probable.

Professor Cope has recently brought some new paleontological evidence to bear on this question, and suggests that the lateral eyes may have arisen from the pineal eye. The condition represented in *Mycterops* is not claimed to necessitate such a view, and there is another interpretation which seems to me admissible, and more in accordance with what we know of the genesis of sense-organs. If the whole median orifice is not to be regarded as a parietal foramen, and if its lateral portions are really orbits as pointed out by Professor Cope, then there seems to be nothing in the way of interpreting the pair of orifices in the plate that divides the orbits as parietal foramina, if the possibility of the double origin of the pineal eye be conceded. Beard has already called attention to the possible existence of a parietal foramen in a corresponding position in *Asterolepis ornatus*.

Leydig's interpretation of the pineal eye is the only one that approaches my view, but it does not carry the origin directly back to invertebrate segmental sense-organs. It must be remembered, however, that Leydig ¹ identifies the lateral-line

¹ Since the above was written, Professor Leydig has published a paper, in which he contends that the pineal organ is not an eye nor a sense-organ of any kind, but a

organs with the sense-organs of the annelids. If an authority of Professor Leydig's standing can be presumed to stand in need of instruction on the differences that divide cerebral from peripheral sense-organs, it is not of course to be expected that my suggestion will meet with a less patronizing reception. These differences have been insisted on so often that they have become common property, and it indicates no small measure of audacity in a critic to assume the role of instructor in regard to them. Take what are now incontestable facts in the phylogeny of annelid and arthropod sense-organs, and add to them the evidences in favor of the common derivation of the vertebrate organs of special sense, and is it not enough to awaken a very strong suspicion that the visual organs of vertebrates will not be able much longer to hold the position of isolation so long conceded to them?

In the study of this question the following points seem to me of first importance: 1. Vertebrate sense-organs must be assumed to be derived from invertebrate sense-organs, and the history of the latter must furnish clues to the genesis of the former. 2. In the development of special senses, visual cells have made the widest departure from the primitive tactile cells. As the derivation of visual cells from cells of the tactile order is now, as I maintain, clearly established by the facts announced in this paper, it follows that structural and functional differences in sensory organs cannot be accepted as proof of diversity of origin. 3. The medullary plate of the vertebrate is undoubtedly an enormous extension of the ancestral invertebrate plate. 4. Sense-organs lying originally outside the neural plate have probably, in consequence of this extension in width, been brought within the medullary area. 5. The ancestral segmental sense-organs were not limited to a single pair of lateral lines, but to several paired lines symmetrically placed on the dorso-lateral and ventro-lateral surface.

19. The caudal ganglia are seven in number, with perhaps a rudimentary eighth. Sometimes from two to four ganglia in front of the caudal group are approximated, and the group thus formed constitutes the anal ganglia. In several American species of Clepsine, however, no such group exists, all the

lymph-sac. This startling announcement is evidently based on extended and careful observations, and it will make it necessary to re-examine the whole ground.

ganglia standing at regular intervals apart. There are generally seven pairs of distinct spinal nerves arising from the caudal ganglia, and sometimes eight.

- 20. The postoral (infra-pharyngeal) ganglia represent five somites, as can be shown in *Clepsine parasitica* and *Branchelliopsis*. Whether one or more somites are represented in the pre-oral (supra-pharyngeal) ganglia, I am not prepared to say. As there are always twenty-one ganglia between the pharyngeal and caudal groups, we have *thirty-three somites represented in the ventral chain* (exclusive of the pre-oral ganglia).
- 21. A careful analysis of the annular composition of the body of *Clepsine* has enabled me to find just *twenty-six* somites in front of the caudal sucker. Adding seven for the sucker, we have thirty-three, which makes the number of somites determined by the external rings agree precisely with the number of ganglia in the ventral chain.
- 22. The assertion by Mr. Apathy that there are six caudal ganglia lacks one of being true; and his statement that there are always three anal ganglia would hit the mark in very few cases indeed. Mr. A. boldly asserts that there are six somites represented in the pharyngeal ganglia. This author does not appear to be aware that the nice balance which he strikes between the head and the tail of a leech is open to any serious objection. For the present I pursue the criticism no further.
- 23. The nervous system of Branchelliopsis presents one feature of exceptional interest. This leech possesses veritable spinal ganglia. These ganglia are lodged in the anterior (sensory) of the two spinal nerves of each somite, at a short distance from the ventral cord. The two nerves issue side by side, but diverge after passing the ganglia of the ventral cord, and then are re-united by a commissure, at the level of the spinal ganglion. Passing the spinal ganglion, the nerves at once subdivide into several branches. One of the main sensory branches runs outward in the anterior wall of the segmental sinus, while another large branch (motor?) runs in the dorsal and posterior wall of the sinus. The pre-sinal branch divides just before reaching the longitudinal muscles, into three branches, the smallest of which appears to end in the muscles, while the two remaining pass on, one to the anterior, the other to the posterior side of the lateral heart, and eventually end in segmental sense-organs.

- 24. A pair of colossal axial nerve-cells are found between every two consecutive ganglia in the ventral cord of Branchelliopsis. The nuclei are very large, and placed about midway between the ganglia. The cells stretch from ganglion to ganglion, but do not pass these limits. Between the brain and the caudal ganglia there are twenty-two pairs, and in both these groups of ganglia the same cells probably occur, for a nucleus, resembling in general appearance the nuclei of the axial cells, is found imbedded close to the root of each nerve. These axial cells undoubtedly correspond to the neurochord cells of other annelids, and probably to the colossal nerve-fibres of Amphioxus, Müller's fibres in Petromyson, and Manthner's fibres in Teleostei. Faivre's intermediate nerve terminates here in the manner described by Hermann for Hirudo, and has nothing whatever to do with the axial cells. Hermann's "median ganglion-cells" are also found in this leech.
- 25. In *Clepsine chelydræ*, the spinal nerves issue from the ventral cord as *three* distinct roots. The anterior, smaller root unites with the middle root, at the lateral edge of the ganglia, and the two then pass on as one nerve, corresponding to the anterior nerve of other leeches.
- 26. The agreement in form and structure between Piscicolaria and the Japanese Branchelliopsis, is remarkable, for it is much closer than that between the fresh-water Piscicola of Europe and marine leeches. Each has three rings to the somite, five pairs of testes, and eleven pairs of nephridia. The testes and nephridia are in corresponding somites in the two forms. I have not thus far succeeded in finding segmental sense-organs in Piscicolaria, but fresh material may bring them to light.
- 27. The nephridial organs of *Branchelliopsis* resemble those of *Clepsine*. Each pair appears to be entirely distinct, and thus to present conditions quite unlike the nephridial net-work described by Bourne in *Pontobdella* and *Branchellion*. For each pair of organs there is a pair of funnels and a pair of external pores. The funnel lies in a diverticulum from the posterior wall of the segmental sinus, in the angle formed by the junction of the segmental with the lateral sinus. A vertical plane cutting a pair of funnels would divide the first ring of the somite into two unequal parts, the posterior of which would be the smaller. A horizontal plane would cut the ventral wall of the

lateral hearts and the dorsal sides of the testes. Its position is thus a little behind the nephridial pore, which opens on the ventral surface a little below the lateral heart, in the anterior half of the first ring.

28. There are four longitudinal vessels and as many sinuses, one dorsal, one ventral, and two lateral. The dorsal vessel is inclosed for the greater part of its length in the dorsal sinus; the ventral vessel lies mostly outside the ventral sinus; the lateral vessels lie just above the lateral sinuses, and run parallel with them. In the post-clitellar region, a pair of branchial vessels are given off in each somite from the lateral vessels. Each branchial vessel divides into two branches, after passing through the muscular strata of the body, one of which passes forward to meet a posterior branch coming from the preceding branchial vessel, while the other passes backward to meet an anterior branch coming from the succeeding branchial vessel. The two branches do not actually meet, but rather each enters separately the base of the auricular chamber of the heart, where the two inflowing currents mingle and ascend to pass through a wide common opening into the main chamber. This opening is on the dorso-lateral face of the chamber, while the efferent opening lies on the ventro-median surface, and leads into the branchial sinus, which opens in turn into the lateral sinus, opposite the junction of the latter with the segmental sinus. The four sinal ostia thus brought together are guarded by peculiar pluriramous muscles. The dorso-ventral sinus communicates with the testicular sinus, and passes into the segmental sinus just before the latter unites with the lateral sinus. The connections between the vessels and sinuses at the ends of the body have not yet been completely traced.

29. All the *Hirudinea* may be derived from a form in which the somite consists of *three* rings. The 5-ring type of *Nephelis* and *Hirudo* has been derived, not from a 6-ring or 12-ring type, but from a 3-ring type, by the acquisition of two new rings. The position of the nephridial pores in the posterior edge of the last ring of the somite, can be accounted for more readily as the result of shifting than of a loss of rings. How three rings can become 4, 5, 6, or 12, I can promise to make clear in an early paper.

30. Copulation in Clepsine is never direct, i.e., by union of

the sexual pores. The spermatozoa are transmitted in spermatophores, which are planted on any part of the exterior, preferably on the back. The gradual contraction of the sperm-case forces the contents through the skin in a steady stream that can be seen under a magnifying power of 20 diameters. By means of sections, I have traced the spermatozoa from the place of entrance to within a few millimetres of the ovaries. The same mode of copulation occurs in Nephelis, and in Peripatus (Sedgwick).

THE LAKE LABORATORY, Milwaukee. Dec. 25, 1888.

